



Review

Improving vegetable quality in controlled environments

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ARTICLE INFO

Keywords:

Biofortification
Eustress
Functional quality
Genetic improvement
Hydroponics
Plant biostimulants
Phytochemicals
Salinity

ABSTRACT

During the last decades, food security has become a vital global concern driven by projections of population increase and exacerbated by the impending pressure of climate change on agriculture. Vegetable crops represent a fundamental ingredient of human diet due to their high nutritional value and bioactive content and could serve towards improving food security and nutritional quality, especially when managed under highly intensified cropping systems in controlled environments. Greenhouse and indoor growing modules not only allow for significantly higher yields compared to open field cropping systems, but also they can facilitate out of season production and substantial manipulation of the chemical composition and bioactive profile of the final product. The present work provides an updated critical overview of scientific advances regarding genotype and microclimate effects on the quality of greenhouse crops. In this context, innovative crop management practices are discussed, including management of the nutrient solution, biofortification and application of plant biostimulants. The review concludes by proposing future research pathways towards enhancing product quality of greenhouse vegetables.

1. Introduction

A primary challenge for modern horticulture is the need to procure food for the increasing global population, projected to reach 10 billion by 2050. At the same time vegetable growers have to cope with sub-optimal crop growth conditions imposed by substantial climate changes (Koevoets et al., 2016). To face these issues, intensive food production systems such as protected cultivation are missioned to increase crop productivity without detrimental effects on quality and sustainability. The advantages of greenhouse and indoor growing modules include: (i) increased off-season vegetable production, (ii) buffering against external weather conditions, and (iii) securing better than outdoor conditions for crop growth and development (Bisbis et al., 2018).

Over the past two decades, demand for quality horticultural products is on the rise, propelled by the growing interest of society in fresh products of high organoleptic, nutritional and functional quality (Bisbis et al., 2018; Kyriacou et al., 2016a). In a recent review, the quality of fresh horticultural commodities was defined as a *dynamic composite of their physicochemical properties and evolving consumer perception, which embraces organoleptic, nutritional and bioactive components* (Kyriacou and Rouphael, 2018). Bioactive compounds present in vegetables, also

known as phytochemicals, can modulate beneficially human metabolism and well-being in general (Ferrari and Torres, 2003). Phytochemicals represent an important source of antioxidant molecules (e.g., phenolic acids, flavonoids, anthocyanins, glucosinolates, tocopherols, ascorbate and carotenoids) able to reduce the risk of cardiovascular diseases and specific forms of cancer, while they stimulate cognitive health (Slavin and Lloyd, 2012).

The synthesis and accumulation of bioactive compounds depend upon many preharvest factors, including genetic material, environmental and microclimatic conditions for plant growth, crop management practices and developmental stage at harvest (Weston and Barth, 1997). However, the genotypic effect is undoubtedly the principle determinant of quantitative and qualitative variation in health-promoting metabolites in vegetables, often surpassing the influence of cultural practices and environmental factors (Kyriacou and Rouphael, 2018; Rouphael et al., 2012a, 2016, 2017c). Efforts are made to enhance key phytochemicals by means of conventional breeding and genetic transformation, but the development of new cultivars with enhanced content in specific functional molecules is still at its infancy, with only a limited number of vegetable cultivars yet released at commercial level (Kyriacou and Rouphael, 2018). Furthermore, disproportional increase

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reaching up to 10–35 fold in some target phytochemicals through genetic selection, including carotenoids, glucosinolates and kaempferol-rutinoside, has raised safety issues as such concentrations have been proved genotoxic (Brusick, 1993; Poiroux-Gonord et al., 2010; Stopper et al., 2005). The manipulation of secondary metabolites through environmental and agronomic factors could be posited as a meaningful compromise between effectiveness and safety, hence it attracts the interest of food and horticulture scientists and quells consumers' concerns regarding genetically transformed and/or modified products (Kyriacou and Rouphael, 2018).

Environmental factors, particularly air temperature and light, and to a lesser extent vapor pressure deficit and carbon dioxide enrichment impact organoleptic and functional quality of greenhouse vegetables, as discussed in the previous review papers of Gruda (2005) and Wang et al. (2008). Among microclimate controls, advanced light-emitting diode (LED) technology is gaining particular popularity with greenhouse growers since it provides optimal management of light conditions (intensity and spectral quality) which can effectively increase the biosynthesis of secondary metabolites in vegetables, including the new class of specialty crop microgreens (Kyriacou et al., 2016a, 2017a). Additionally, the management of nutrient solution can be instrumental in influencing yield and quality of greenhouse vegetables. In this respect, hydroponic cultivation systems (i.e., substrate culture, nutrient film technique, floating system) facilitate the precise control of plant nutrition, thus modulating the levels of bioactive compounds (Borgognone et al., 2016; Fanasca et al., 2006a, b; Fallovo et al., 2009a, b; Lucini et al., 2016). The application of an *eustress* (positive stress), such as moderate salinity or nutritional stress, by managing the concentration and composition (cationic and anionic proportions or single ions) of the nutrient solution, can be practical and effective in improving the nutritional value of vegetables and in reducing the accumulation of anti-nutrient compounds, such as nitrates (Colla et al., 2018; Kyriacou and Rouphael, 2018; Tomasi et al., 2015). Soilless culture can also be effective in the biofortification of edible plant portions with essential and/or beneficial micronutrients to human health (Tomasi et al., 2015; White and Broadley, 2005).

Accordingly, the present review aims at providing an updated overview of scientific advances addressing genotypic and microclimate management effects (air and root zone temperature, light conditions, CO₂ enrichment and vapor pressure deficit) on the quality of greenhouse crops. Moreover, innovative crop management practices are discussed in the same context, including management of the nutrient solution concentration and composition, biofortification and the application of plant biostimulants. The review concludes by identifying several possibilities for future research to enhance product quality of greenhouse vegetables.

2. Genotypic and grafting effects on the quality of greenhouse crops

In the past decades, breeding for field and greenhouse cultivars has prioritized yield improvement, disease resistance and extended post-harvest life (Bai and Lindhout, 2007; Dorais et al., 2008; Gil, 2015; Klee and Tieman, 2013). Arguably, breeding for these characters has been made at the expense of nutritional value and sensory quality; for instance, breeding for longer shelf-life has resulted in undesirable pleiotropic effects on organoleptic attributes (Causse et al., 2002; Davis et al., 2004). In breeding efforts, quality has featured mainly in reference to key first-level attributes, such as size, shape and color, which can influence momentary purchase decisions.

Genotype selection is the key determinant of organoleptic quality and functional properties of fruits and vegetables, particularly for greenhouse crops where agronomic (e.g., irrigation and fertilization) and environmental factors (e.g., light, temperature and atmospheric CO₂) are largely controlled (Kyriacou et al., 2017a; Rouphael et al., 2012a). Optimal growth conditions provided by fully controlled

greenhouse environments highlight further the dominant role of genotype selection for the quality of harvested vegetables. Genotype effect on the sensory quality and phytonutrient composition of greenhouse vegetables may surpass that of the origin of the products as well as the effect of brief postharvest storage under optimal conditions (Nassar et al., 2015). Strong determinants for cultivar selection of greenhouse vegetables include the levels of minerals (particularly Cu, Fe, K, Mg, and P), carotenoids (β -carotene, lycopene, and lutein), carbohydrates, organic acids, phenols, anthocyanins, flavonoids, flavonols and ascorbic acid (Dorais et al., 2008; Nassar et al., 2015).

Collecting desirable genotypic traits while avoiding undesirable ones can be further enhanced by grafting, which facilitates independent selection of rootstock and scion traits. A comprehensive critical review of the effects of grafting on the configuration of fruit quality in vegetable crops, and the biological mechanisms implicated, has been recently produced by Kyriacou et al. (2017b). Initially adopted as an alternative to the use of chloro-fluorocarbon soil fumigants, the grafting of annual fruit crops is no longer restricted to the management of soilborne diseases and has become the mainstream, particularly for *Cucurbitaceae* and *Solanaceae* crops (Kyriacou et al., 2017b). Grafting is increasingly employed for ameliorating abiotic and biotic stresses on vegetable crops, by tapping wild genetic resources for root physiological tolerance to stress conditions of salinity, nutrient stress, water stress, organic pollutants and alkalinity (Savvas et al., 2010; Schwarz et al., 2010; Borgognone et al., 2013). The significant yield increase incurred by selecting vigorous commercial rootstocks has encouraged their use under protected cultivation where distribution of infrastructural and energy costs is highly dependent on productivity (Colla et al., 2011). Under soil biotic and abiotic stress conditions, rootstock effects on plant performance clearly outweigh those of the scion; however, rootstock effects on scion fruit quality must also be considered (Kyriacou et al., 2017b). These may be mediated by changes in water and nutrient uptake efficiency, by changes in ripening behavior due to altered source-sink balance, and even by epigenetic factors involving transfer of genetic material from rootstock to scion (Avramidou et al., 2015; Savvas et al., 2010; Soteriou et al., 2014).

Incompatibility and deterioration of fruit quality are much more common problems with melon (*Cucumis melo*) than watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] grafting, particularly with *Cucurbita* hybrid rootstocks (Guan et al., 2014; Kyriacou et al., 2017b; Traka-Mavrona et al., 2000; Soteriou et al., 2016). These problems are exacerbated by widespread rootstock-scion interaction owing to the broad genetic-physiological basis of melon botanical varieties, ranging from the odorous climacteric varieties *cantalupensis* and *reticulatus* (e.g. charentais and muskmelon) to the non-aromatic non-climacteric *inodorus* varieties (e.g. honeydew and canary) (Pech et al., 2008; Allwood et al., 2014). For example, the fruit weight of greenhouse muskmelon and honeydew melon was either increased or not affected by various *C. melo* and interspecific commercial rootstocks, as rootstock-scion interaction underscored these effects (Condurso et al., 2012; Colla et al., 2010; Crinò et al., 2007; Verzera et al., 2014). Variable rootstock-mediated responses of melon types have also been reported for pulp texture. Interspecific and *C. melo* rootstocks had no effect on honeydew dry matter content and pulp firmness (Crinò et al., 2007), but reduced Cantaloupe (Zhao et al., 2011), and also Galia and Ananas melon pulp firmness (Soteriou et al., 2016). Rootstock-scion interaction also affected fruit soluble solids content (SSC) and organoleptic rating of greenhouse melon, but both negative and positive effects were generally limited in scale and impact on overall fruit quality (Crinò et al., 2007; Guan et al., 2014; Soteriou et al., 2016; Traka-Mavrona et al., 2000; Trionfetti-Nisini et al., 2002; Verzera et al., 2014).

Watermelon is the most ubiquitously grafted annual crop, grown however predominantly under open field conditions and marginally under greenhouse conditions for out-of-season or early production (FAO, 2012). Numerous works have examined the implications of grafting for watermelon quality but most refer to open field conditions.

In the case of greenhouse mini watermelon, scions grafted on interspecific rootstocks incurred significant increase in fruit weight and rind thickness, compared to the non-grafted controls, but fruit shape was not affected (Colla et al., 2006a). The SSC of watermelon fruit is generally not influenced by grafting on commercial *C. maxima* × *C. moschata* rootstocks (Colla et al., 2006a), however potential delay in fruit maturation must be considered (Soteriou et al., 2014). On the other hand, watermelon pulp firmness is the quality parameter most consistently increased in response to grafting, provided rootstock-scion compatibility (Kyriacou et al., 2016b, 2017b).

In the case of greenhouse cucumber (*Cucumis sativus* L.) increase in fruit weight may be obtained with *Cucurbita* interspecific rootstocks, compared to non-grafted control (Colla et al., 2012, 2013b; Goreta Ban et al., 2014), but no effect is noted on fruit firmness (Sakata et al., 2007; Colla et al., 2013a). Higher SSC and decrease in titratable acidity (TA) was mediated by interspecific rootstocks (Colla et al., 2013b), whereas the use of figleaf gourd (*C. ficifolia*) as a rootstock reduced the SSC (Lee et al., 1999). In addition, grafting on *Lagenaria siceraria* rootstocks may modify the volatile profile of both peel and flesh of cucumber fruit (Guler et al., 2013).

Grafting tomato (*Solanum lycopersicum* L.) plants for production under protected environment is becoming the mainstream practice with the effects of grafting on tomato fruit quality being generally moderate compared to grafted cucurbits (Kyriacou et al., 2017b). Vigorous interspecific rootstocks have been credited with increase in fruit weight (Krumbein and Schwarz, 2013; Pogonyi et al., 2005; Schwarz et al., 2013; Turhan et al., 2011), while less vigorous rootstocks have been attributed with reduced fruit weight (Schwarz et al., 2013). Rootstocks such as ‘Brigeor’, ‘Maxifort’ (*S. lycopersicum* L. × *S. habrochaites* S. Knapp & D.M. Spooner) and LA1777 (*S. habrochaites* S. Knapp & D.M. Spooner) can increase total yield and visual quality of fruit by reducing the incidence of blossom-end-rot (Fan et al., 2011b; Krumbein and Schwarz, 2013; Schwarz et al., 2013; Ntatsi et al., 2014). This effect is mainly rootstock-dependent, but also subject to rootstock × scion × environment interaction that affects nutrient and water uptake (Kyriacou et al., 2017b). Moderate loss of fruit firmness seems to be the predominant rootstock effect on grafted tomato, despite the demonstrated increase in Ca uptake and fruit content (Khah et al., 2006). Reported rootstock effects on taste parameters, such as SSC and TA, are variable but of limited scale compared to the scion impact, since the organoleptic value of tomato fruits appears not to be significantly influenced by rootstock or self-grafting of the scions (Barret et al., 2012; Kyriacou et al., 2017b). Grafting on interspecific hybrids may affect the levels of odour-active fruit volatiles but further work is warranted in interpreting these effects (Krumbein and Schwarz, 2013).

The most common rootstock for eggplant (*Solanum melongena* L.) is *Solanum torvum*, but numerous other species and interspecific hybrids have served as eggplant rootstocks (Lee et al., 2010; Khah, 2011; Gisbert et al., 2011; Moncada et al., 2013; Sabatino et al., 2016). Rootstock effects on eggplant fruit quality lack consistency owing to widespread rootstock-scion interaction, differing experimental environments, and failure to standardize fruit harvest maturity (Kyriacou et al., 2016b; Kyriacou et al., 2017b). Grafting effect on greenhouse eggplant fruit weight is generally non-significant (Khah, 2011). However, loss of fruit firmness has been reported with grafting on *S. torvum* and *S. sisymbriifolium*, (Cassaniti et al., 2011; Arvanitoyannis et al., 2005). Grafting on *S. torvum* had no significant effect on eggplant taste parameters such as SSC and TA (Lee et al., 2010), or on eggplant grafted onto *L. hirsutum* and *L. esculentum* rootstocks (Khah, 2011).

Pepper (*Capsicum annuum* L.) grafting is yet practiced on a limited scale and reports on the implications of this practice for fruit quality remain scarce (Schwarz et al., 2010; Penella et al., 2016). Rootstocks used are mainly select cultivars of *C. annuum*, (Lee et al., 2010). Decrease in pepper fruit weight is usually an indicator of rootstock-scion incompatibility (Gisbert et al., 2010), whereas moderate increase in fruit weight (Doñas-Uclés et al., 2014) or no weight changes (Colla

et al., 2008) are the most common responses to compatible *C. annuum* rootstocks. In addition, positive or no effects on fruit SSC were identified in pepper grafted on *Capsicum* rootstocks (Colla et al., 2008; López-Marín et al., 2013). Increase in antioxidant capacity and β-carotene content, but not in lycopene (Chávez-Mendoza et al., 2013) or phenolic content (Chávez-Mendoza et al., 2013; López-Marín et al., 2013; Sánchez-Torres et al., 2016) was also identified in relation to pepper grafting, whereas rootstock effect on ascorbic acid content was limited compared to that of scion genotypes (Kyriacou et al., 2017b).

3. Microclimate factors affecting greenhouse vegetable quality

Greenhouse cultivation of vegetables is crucial, as it allows for controlled environmental conditions and therefore for high revenue out-of-season production. Modern greenhouses are designed and equipped with sensors and automated controlling systems to adjust air and root-zone temperature, light intensity and quality (i.e. wavelength), relative humidity and carbon dioxide (CO₂) concentration, according to plant requirements and phenological growth stage. Apart from facilitating improved and out-of-season vegetable production, management of the greenhouse environment is a useful toolbox for boosting the sensorial and functional components of vegetable quality associated with pre-harvest conditions (Lee and Kader, 2000).

3.1. Air and root-zone temperature

The scientific literature abounds with reports on the significance of temperature control for vegetable quality. According to Schonhof et al. (2007), the combined effect of elevated air temperatures and low radiation may have a beneficial effect on glucosinolates, ascorbic acid and lutein content of greenhouse broccoli. Although high temperatures are beneficial on plant growth and yield, temperatures exceeding species-specific thresholds have deleterious effects on plant development and product quality, since they generate nutrient and hormone imbalances, protein misfolding and loss of radical scavenging activity (Giri et al., 2017; Liu et al., 2016; Mansour et al., 2009; Zhou et al., 2014). In the study of Max et al. (2009), the effect of cooling on tomato fruit quality under tropical conditions was studied and it was reported that fan and pad cooling in polyethylene covered greenhouses decreased the incidence of blossom end rot and undersized fruit, as well as increased Ca content, while mechanical ventilation in net covered greenhouses decreased the incidence of fruit cracking. Quality features of tomato fruit that have been strongly correlated with cumulative temperature (the sum of daily temperatures above a specific temperature threshold over the growing period; T_{cum}) within a greenhouse environment, include fruit firmness, electrical conductivity (EC) of fruit juice, SSC and phenolic compounds content, whereas dry matter and ascorbic acid content as well as TA and pH of juice were not correlated with T_{cum} (Riga et al., 2008). Moreover, lycopene biosynthesis in tomato fruit is inhibited at temperatures below 12 °C and above 32 °C (Kläring et al., 2015), while the night/day temperature differential is also important for carotenoid synthesis, lycopene in particular (Dumas et al., 2003). However, according to Gautier et al. (2008), temperatures within the range of 21 and 26 °C decreased total carotenoids but not lycopene content, whereas only higher temperatures (27–32 °C) had a detrimental effect on lycopene content and its precursors, namely phytoene, phytofluene, and neurosporene.

Although air temperature is crucial for plant development and vegetable quality, root-zone temperature is equally important under greenhouse conditions. Urrestarazu et al. (2008) have suggested that heating of nutrient solution in soilless cultivation systems may increase not only yield and early production of melon fruit, but also SSC (°Brix) content, an essential quality feature for the marketability of the final product. Moreover, according to Cabañero et al. (2004) root zone temperatures of 35 °C resulted in higher calcium uptake by pepper plants and consequently in mitigation of negative salt effects and

blossom end rot incidence in fruit. In contrast, root temperatures higher than 20 °C have negative effects on tomato fruit quality, whereas for fast growing vegetables they have beneficial effects (Adams, 1999). In the same line, Kafkafi (2001) and Tindall et al. (1990) reported that increasing nutrient solution temperature from 12 to 20 °C increased water flow through the stems of tomato plants by 250% which consequently results in higher nutrient uptake and better fruit quality.

Apart from the direct effects, temperature may also have indirect implications for vegetable quality, since passive heating under controlled environments has been reported to decrease incidents of *Sclerotinia sclerotiorum* and *Botrytis cinerea* on sweet basil plants (Elad et al., 2017), probably by conferring higher plant resistance to the pathogens rather than inflicting direct lethal effects on the pathogens.

3.2. Light conditions

Light conditions within a greenhouse are significantly influenced by cover materials, with recent advances in materials design allowing producers to achieve targeted light conditions through selection of cover material specifications. Apart from protection against environmental conditions and biotic factors, greenhouse cover materials are useful towards the modification of light conditions by either filtering solar radiation through photo-selective film covers, or simply by reducing light intensity through shading nets. In any case, cover materials are strongly associated with vegetable quality.

3.2.1. Light quality

Greenhouse light conditions are crucial for vegetable quality in terms of either visual and/or organoleptic properties and chemical composition. Carotenoid biosynthesis is highly dependent on light conditions (intensity and quality) and on direct exposure of fruit to light, given that optimal temperatures range between 12–32 °C (Dumas et al., 2003). Flavonoid content is also affected by light quality, since the absence of UV-B radiation within a glasshouse decreases the rate of polyphenol biosynthesis in leafy vegetables, bearing a direct impact on flavor and visual appearance (Gruda, 2005). According to Li and Kubota (2009) and Lin et al. (2013), the application of variable quality supplemental light (UV-A, blue, green, red and far-red, and white LED diodes) elicited significant differences in phytochemicals content (anthocyanins, carotenoids, chlorophylls and flavonoids) of lettuce leaves, hence supplemental light could be a useful modulator of phytochemical content.

Taulavuori et al. (2016) and Ouzounis et al. (2015) studied the effect of enhanced blue light on green and red lettuce quality and observed a significant increase of the main phenolic compounds (cichoric acid, quercetin and their derivatives) and pigments, under prolonged periods of light supplementation, while Hao et al. (2012) and Hovi-Pekkanen and Tahvonon (2008) reported that interspersed treatment with red, blue and white lamps improved the visual quality of cucumber fruit. The ratio of red:blue spectra may also affect the quality of leafy and fruit vegetables, with ratios of 0.7 being beneficial for phenolic compounds and flavonoids content, antioxidant activity and nitrates content of basil leaves and strawberry fruit (Piovene et al., 2015), and red lettuce leaves (Johkan et al., 2010). Supplementary lighting has been reported to affect microgreens nutritional quality, since according to Samuolienė et al. (2012a) and Samuolienė et al. (2016) the short-term application of red light for 3 days prior to harvest increased significantly the total phenolic, total anthocyanin and ascorbic acid contents, as well as the antioxidant activity for most of the studied microgreens. Ohashi-Kaneko et al. (2007), Fu et al. (2012) and Długosz-Grochowska et al. (2016) suggested that light manipulation within the greenhouse environment could be used as a means to improve the quality of leafy vegetables, mostly by reducing nitrate and by increasing ascorbic acid, folate, polyphenol and chlorophyll content, while Samuolienė et al. (2012b) and Samuolienė et al. (2013b) reported that supplementary green and blue LED diodes may increase antioxidant

components (vitamin C, phenolic compounds and tocopherols content) in red, green, light green and romaine baby leaf lettuce. Conclusively, further investigation is warranted to determine the physiological, biochemical and molecular changes linked to these modifications and also to identify the optimal light quality that boost specific bioactive components in vegetables.

According to Ilić et al. (2012) and Ilić and Fallik (2017), covering plastic greenhouses with photo-selective nets of different colors and shading efficiency had a significant effect on tomato fruit quality by reducing the incidence of sun-scalding and fruit cracking, compared to unshaded greenhouses and field grown tomatoes. In addition, colored nets improved fruit color, through higher content in β -carotene and lycopene, and also antioxidant compounds in tomato (Díaz-Pérez, 2014) and pepper fruit (Milenković et al., 2012). In similar studies of Tinyane et al. (2013) and Ilić et al. (2015), the use of pearl photo-selective nets improved significantly the overall fruit quality and shelf-life of tomato cultivar 'AlfaV'. The use of red and pearl nets increased the volatile fraction and aroma of tomato fruit compared to black nets (Tinyane et al., 2013; Selahle et al., 2014). Near infrared ray (NIR)-cutting nets may increase total soluble sugars and sucrose content in melon fruits, since strong absorption of NIR and high transmittance of visible light result in lower temperatures, hence lower sugar degradation (Stagnari et al., 2015). The beneficial effects of NIR-blocking and UV-blocking covers on pepper (Kittas et al., 2006), eggplant (Lamnatou and Chemisana, 2013) and tomato (Živanović et al., 2017) fruit quality have been also confirmed. Modulating spectral bands through the use of nets with different colors may affect ripening-related gene expression (Bergquist et al., 2007; Mashabela et al., 2015), while photo-selective covers may also impact pest physiology and population dynamics (Ben-Yakir et al., 2012; Makled et al., 2012; Shahak et al., 2008).

3.2.2. Light intensity

Management of light intensity within controlled environments is of major importance considering its implications for photosynthetic activity and the chemical composition of vegetables (Kyriacou et al., 2016a). Depending on cultivation facilities, the means for controlling light intensity differ between greenhouses, screenhouses and entirely enclosed facilities (Bian et al., 2015). In any case, excessive amounts of light are associated with damages in photosynthetic system II and photoinhibition which result in excessive amounts of energy that cannot be channeled through the biosynthetic processes (Ksas et al., 2015). Loss of firmness and fruit scalding in tomato fruit have been associated with light intensity at levels that exceed the photosynthetic saturation threshold and raise the fruit temperature through direct exposure to light radiation (Sams, 1999). Moreover, injuries from direct solar radiation may affect fruit ripening of tomato fruit since they interfere with ethylene production and pigment formation, while they can promote pathogen attacks due to ruptures in the texture of the pericarp (Dumas et al., 2003).

Various molecules are considered to have defensive role against high light intensities, including carotenoids, tocopherols and plastoquinones that are responsible for quenching high-light induced reactive oxygen species (ROS; Havaux et al., 2005; Hideki et al., 2016; Krieger-Liszak and Trebst, 2006). Moreover, increased irradiance improved the levels of ascorbate, carotenes and phenolic compounds (rutin and caffeic acids), without however affecting the reducing sugars content (Gautier et al., 2008). The same authors suggested that higher contents of ascorbate and phenolic compounds could be attributed to increased activity of specific biosynthetic enzymes, such as ascorbate peroxidase, dehydroascorbate reductase, and monodehydroascorbate reductase in the case of ascorbate, and chalcone synthase in the case of rutin. They further proposed that the increase in carotenes resulted from enhancement of carotenogenesis through the modulation of phytoene synthase.

In the same line, light intensity affects nitrate and vitamin C contents of leafy vegetables, since nitrate reductase activity necessary for

nitrate assimilation is triggered by high light intensities (Petropoulos et al., 2011, 2008), while increased solar energy results in higher rates of sugars and consequently of vitamin C biosynthesis (Lee and Kader, 2000). Moreover, increasing light intensity between 330 and 440 mmol m⁻² had positive effects on carotenoids, total phenols and zeaxanthin contents and antioxidant activity of various *Brassica* microgreens, while light intensities beyond or above these limits had either negative or no impact on nutritional value (Craver et al., 2017; Samuolienė et al., 2013a). Similar results have been reported by Lefsrud et al. (2008) and Li et al. (2009) who suggested that light intensity affects carotenoids content in spinach and kale leaves. However, they indicated that light requirements for maximizing carotenoids contents are species-specific and a generalized recommendation is not applicable. In addition, Wu et al. (2007) studied the effect of variable light intensities on the quality of broccoli shoots and they suggested that transition from high (350 mmol m⁻² s⁻¹) to low (41 mmol m⁻² s⁻¹) light intensities may increase carotenoids, glucosinolates, macro and micronutrients contents. Light intensity affects the quality not only of leafy but also fruit vegetables. Kläring and Krumbein (2013) indicated that reducing light intensity decreased growth and yield of tomato plants, as well as β -carotene; however, dry matter, sugars and lycopene levels were not affected by constraining light intensity, whereas fruit TA increased. Shelf life and metabolism of daikon radish microgreens and spinach leaves were also negatively affected by exposure to low light intensity which induced post-harvest yellowing, withering and overall downgrading of visual quality, as well as decline in L-ascorbic acid content (Toledo et al., 2003; Xiao et al., 2014). Jarquín-Enríquez et al. (2013) also reported that tomato lycopene content and fruit color were improved in greenhouses covered with double-layer polyethylene films compared to glasshouses painted with 15% CaCO₃ solution.

By contrast, Krumbein and Schwarz (2013) observed a significant effect of shading (50% reduced light transmission) on grafted tomato fruit quality, expressed in lower β -carotene and sugars content, and higher TA, while they also recorded differences in aroma profile between shaded and non-shaded fruit. In the same study, grafting technique and rootstock-scion combinations did not alleviate the negative effects of shading on fruit quality.

Apart from fruit vegetables, shading nets have also shown significant results in leafy vegetables quality, where according to Stagnari et al. (2015), the combination of nets providing 0.9% reduction in photosynthetically active radiation (PAR) and nitrogen application rate of 185 kg ha⁻¹, reduced the nitrate content in lettuce leaves, while further reduction of PAR resulted in lower total phenolic content and antioxidant activity. Colored shading nets may have a beneficial effect on aroma attributes of leafy and aromatic vegetables, since according to Buthelezi et al. (2016) the use of red and pearl nets increased aromatic compounds content in coriander and marjoram plants. Using clear plastic film vs. light-diffusing plastic film covers was beneficial to lettuce quality, as heads were more compact and contained less nitrates (Riga and Benedicto, 2017). Colored cover films may increase chlorophyll and dry matter content in chard leaves (*Beta vulgaris* L. var. *cicla*), thus improving visual quality and taste (Casierra-Posada et al., 2015). In addition Becker et al. (2013) reported that the use of energy saving screens at early growth stages does not affect yield and quality (flavonoids and soluble sugars content) of lettuce, while at the same time it lowers substantially the energy consumption for greenhouse heating. Moreover, the cultivation of lettuce plants under black or blue shading nets increased chlorophyll content, compared to open field cultivated plants (Ilić and Fallik, 2017), and similar increases were observed in fruit vegetables such as pepper (Alkalai-Tuvia et al., 2014; Díaz-Pérez, 2014; Ombódi et al., 2016).

Light intensity may therefore modulate phytochemicals and visual quality of vegetables before but also after harvest. Further studies should define species- and even genotype-specific optimal light requirements with respect to the sensory and functional quality of the final product.

3.3. CO₂ enrichment

The increase of carbon dioxide (CO₂) concentration through enrichment to levels up to 1000–1200 μ mol mol⁻¹, is a common practice for greenhouse cultivation to increase yield and earliness (Chalabi et al., 2002). However, its application is highly dependent on environmental conditions, e.g. temperatures that allow for prolonged closure of ventilators, as well as on greenhouse structure, cultivation intensity and market value of the final product that all together can compensate for higher production costs. So far, the studies about CO₂ enrichment in greenhouse environment focus mostly on fruit vegetables and lettuce, where apart from yield increase up to 30%, a significant effect on chemical composition has been also reported. CO₂ enrichment up to 1000 μ mol mol⁻¹, resulted in higher content of flavonoids and caffeic acid derivatives in two red lettuce cultivars, while higher flavonoid content could be explained by the increase in sugars which serve as precursors in flavonoids biosynthesis (Becker and Kläring, 2016). Red lettuce cultivars appear more responsive to elevated CO₂ than the green ones, showing a higher content in secondary metabolites and antioxidant activity (Sgherri et al., 2017). A negative effect of elevated ambient CO₂ was observed in lettuce plants inoculated with arbuscular mycorrhizal fungi, as increased photosynthates were antagonistically consumed for shoot growth and mycorrhizal colonization instead of serving leaf biosynthetic activity (Baslam et al., 2012).

Elevated CO₂ has a significant effect on fruit vegetables, such as tomato. Khan et al. (2013) observed a beneficial effect mostly on sugars (total, reducing and non-reducing), and less so on fiber content, and a negative effect on vitamin C, protein, organic acids, fat and ash contents. Mineral composition was also affected and a variable response depending on genotype and specific elements was reported, while the same trend was observed in fatty acids composition. In contrast, Jin et al. (2009) have reported that CO₂ enrichment via composting of crop residues and animal manure within the greenhouse environment, resulted in a significant increase of sugars and ascorbic acid, as well as a decrease of nitrate content in leafy vegetables such as celery (*Apium graveolens* L.), leaf lettuce (*Lactuca virosa* L.), stem lettuce (*Lactuca sativa* L.), oily sowthistle (*Sonchus oleraceus* L.), and Chinese cabbage (*Brassica chinensis* L.), indicating a beneficial effect on final product quality.

3.4. Vapor pressure deficit

Air humidity is expressed either as relative humidity (% RH) or as vapor pressure deficit (kPa VPD). High RH or low VPD result in heat damage due to reduction in evapotranspiration rates, the main cooling mechanism of plants, while at the same time the reduction in sap flow through the phloem reduces translocation of ions within plant tissues and results in nutrient deficiency symptoms and lower visual quality (Gruda, 2005). Moreover, high RH results in high turgor pressure, which may increase tomato fruit cracking especially at night, and light coloring and malformation of cucumber fruits (Bakker et al., 1987; Leonardi et al., 2000). The use of fogging system as a means to increase RH in screenhouses has been reported to increase lycopene and organic acid content, and antioxidant activity of tomato fruit, compared to open field, screenhouses without fogging system, and screenhouses with fogging system and plastic covering (Leyva et al., 2014). Similar results regarding the effect of low VPD on lycopene content of cherry and salad tomato fruit have been reported by Leonardi et al. (2000) and Rosales et al. (2011). High VPD usually coincides with high temperatures and solar radiation, all together inducing oxidative stress with severe negative effects on marketable yield, carotenoid and mineral contents, whereas phytonutrients, antioxidant activity, and sugars contents increase (Gent, 2007, 2008; Rosales et al., 2011). According to Xu et al. (2007), high VPD lowers chlorophyll and soluble proteins content in tomato fruit, while RuBisCo (ribulose-1,5-bisphosphate carboxylase/oxygenase) activity was also reduced along with lower photosynthetic capacity. In the same study, it was suggested that adjusting VPD at

relatively low levels (corresponding to a transpiration rate of 800 ml of water per plant, per day) and enhances fruit quality (sugar content, fruit color, and low incidence of fruit malformation). Vanhassel et al. (2015) observed that high RH at night reduces the incidence of tipburn on lettuce leaves, since root pressure increases translocation of Ca to non-transpiring leaf tissues and alleviates Ca deficiency symptoms, such as tipburn. Therefore, the control of air humidity within the greenhouse environment is a useful practice for retaining high visual quality of both fruit and leafy vegetables, while at the same time it may affect phytochemical composition and antioxidant potential.

4. Innovative crop management practices

4.1. Salinity as eustress for improving greenhouse vegetable quality

Manipulation of bioactive molecules and secondary metabolites in vegetables by management of the nutrient solution is a research area attracting the interest of growers, extension specialists as well as food scientists (Kyriacou and Rouphael, 2018). In this respect, hydroponic cultivation systems (i.e., substrate culture, nutrient film technique, floating system) present a sustainable tool that facilitates the precise control of plant nutrition (Rouphael and Colla, 2009; Rouphael et al., 2012a). Compared to soil culture, hydroponics provide the possibility to modulate bioactive compounds through appropriate control of nutrient solution composition (cationic and anionic proportions), chemical forms of the elements, and also salinity and EC (Borgognone et al., 2016; Fanasca et al., 2006a, b; Fallovo et al., 2009a, b; Lucini et al., 2016).

The application of an *eustress* (i.e., positive stress) such as mild to moderate salinity or nutrient stress can be easily applied by managing the concentration and composition of the nutrient solution to improve the nutritional value of vegetables as well as reducing the accumulation of undesired compounds (Colla et al., 2018; Kyriacou and Rouphael, 2018; Tomasi et al., 2015). In fact, in response to such a practice, vegetable crops will activate several physiological mechanisms to cope with sub-optimal conditions related to *eustress*. Such mechanisms involve the synthesis and accumulation of bioactive metabolites (ascorbate, carotenoids, glucosinolates, phenols, polyamines and phenols) able to enhance the tolerance of vegetables to abiotic stresses (Orsini et al., 2016). As bioactive molecules command key roles in human body's nutrition physiology, they contribute an added value to basic nutritional attributes of vegetables (Erba et al., 2013; Lairon, 2010; Rouphael et al., 2017a).

Several studies demonstrate the beneficial effects of elevated nutrient solution EC on the sensorial and functional quality traits of important vegetable crops such as tomato (Dorais et al., 2008; Schwarz et al., 2009). Increasing the EC of the nutrient solution to 6.5 dS m^{-1} and especially 10 dS m^{-1} led to increase on a fresh weight basis in β -carotene, lycopene and phenolics by 35%, 65% and 20%, respectively, in comparison to the control treatment ($\text{EC} = 3 \text{ dS m}^{-1}$). However, no significant differences were recorded when results were expressed on a dry weight basis, also indicating a significant effect on water content of the final product. Therefore, salinity effects on health-promoting compounds accounted on a fresh basis could simply reflect a concentration effect and active accumulation (Zushi and Matsuzoe, 2015). Similarly, Wu et al. (2004) showed that by increasing salinity from 2.4 to 4.5 dS m^{-1} a significant increase in lycopene content (34–85%) on a fresh weight basis was incurred in four cultivars of tomato (Blitz, Mariachi, Quest and Rapsodie). A positive effect on lycopene (6%), vitamin C (9%) and total phenolics content (8%) on fresh weight basis by increasing EC from 2.2 to 4.5 dS m^{-1} has been also described in a recent study conducted by Moya et al. (2017). Ehret et al. (2013) also reported an increase of antioxidant molecules, e.g., β -carotene, lycopene, and vitamin C in greenhouse tomato treated continuously with nutrient solution EC of 4 and especially 6 dS m^{-1} . However, multiple regressions of antioxidants in relation to EC and climatic factors showed

that antioxidants responded more strongly to light and temperature than to EC (Dorais et al., 2008; Schwarz et al., 2009). Borghesi et al. (2011) highlighted that increments in tomato carotenoids achieved by adding 35 mol m^{-3} NaCl ($\text{EC} = 5.5 \text{ dS m}^{-1}$) to the nutrient solution were similar to or even higher than those obtained by genetic engineering. In the same study, increasing the EC of the nutrient solution from 3.5 to 5.5 dS m^{-1} increased the lycopene, β -carotene and lutein contents by 1.1–3, 1.16–1.53 and 1.02–2.35 fold, respectively, depending on the genotypes tested ('Ailsa Craig', Anthocyanin fruit type, 'Atroviolaceum' and 'Sun Black'). Moreover, saline treatment increased the accumulation of an important secondary metabolite such as anthocyanin in fruits of Sun Black (2-fold increase), whereas an opposite trend was observed in fruits of Anthocyanin (10-fold decrease; Borghesi et al., 2011). A presumed mechanism involved in the synthesis and accumulation of lycopene under moderate salt stress might involve the up-regulation of genes encoding enzymes involved in the key steps of lycopene biosynthesis (Giuliano et al., 1993). On the other hand, several authors reported that the effective threshold for nutritional quality could be highly influenced by the magnitude of the stress (concentration and time of exposure) as well as the plant genotype $\times$ environment interaction (Dorais et al., 2008). For instance, Shi et al. (2002) reported that moderate salinity stress did not affect several secondary metabolites in tomato such as ascorbic acid, α -tocopherol, lycopene and lutein. Also Dorais et al. (2000) demonstrated a sharp decrease in β -carotene and ascorbic acid when greenhouse tomato plants were grown with NaCl and NaCl/KCl (1:1) in the nutrient solution. This inhibition effect could be attributed to the use of non-tolerant cultivars as well as to climate factors (temperature and solar radiation). It is well established that high fruit temperatures ($> 32^\circ\text{C}$) can degrade and impede lycopene synthesis (Taber et al., 2008); similarly, vitamin C declined with high temperature in tomato fruits (Lester, 2006). The NaCl-mediated decrease in leaf area may have modified the temperature and light conditions of the fruit, and thereby indirectly reduced the phytonutrients content (Dorais et al., 2008; Kyriacou and Rouphael, 2018).

Adding NaCl to nutrient solution is normally accompanied by an increase in flavor compounds including organic acids, sugars and volatiles (Auerswald et al., 1999). For tomato, flavor improvement (high SSC and TA) starts from an EC of 3 dS m^{-1} in nutrient solution (Auerswald et al., 1999); however, this threshold depends on environmental conditions. Increased SSC content and/or TA in fruits from salt-stressed plants has been reported for tomato (Krauss et al., 2006; Moya et al., 2017; Pasalic et al., 2016; Zushi and Matsuzoe, 2015), cucumber (Colla et al., 2012, 2013b), melon (Colla et al., 2006a; Rouphael et al., 2012b), watermelon (Colla et al., 2006b), pepper (Colla et al., 2006c; Marin et al., 2009), zucchini squash (Rouphael et al., 2010, 2017b) and eggplant (Savvas and Lenz, 1996). The increase in SSC and/or TA in vegetable fruits grown under high EC levels could be associated with a lower water accumulation of water in vegetables due to an osmotic effect of the higher salinity nutrient solution (De Pascale et al., 2001).

In a recent study, Zushi and Matsuzoe (2015) investigated the metabolic profile of greenhouse tomato fruit under different salt intensities (0, 25, 50, 75 and 100 mM NaCl). Both sucrose and citric acid contents increased, on both fresh and dry weight bases, in salt-stressed fruits in comparison to the no-salt control. The authors attributed the higher levels of both compounds to upregulation of the sucrose transporter under salt stress conditions. Other authors, reported that the increase in sucrose level could be caused by inactivation of cell wall invertase due to pH changes in the apoplast as well as by sodium accumulation in the cell wall (Pressey, 1994).

The beneficial effect of mild salt stress application on nutritional value, chemical composition and bioactive compounds was also reported on other important greenhouse vegetables such as pepper and strawberry (Cardenosa et al., 2015; Marin et al., 2009). Marin et al. (2009) demonstrated an enhancement in SSC and TA as well as in vitamin C in green and red-turning pepper when salinity increased from 0 to 30 mM NaCl. Similarly, in strawberry the SSC and total phenols

contents and antioxidant activity increased with the application of NaCl (Cardenosa et al. 2015). The biosynthesis and accumulation of phenolic compounds has been described as actively involved in the neutralization of free radicals for coping with oxidative stress (Grace, 2005). Interestingly, Cardenosa et al. (2015) reported that salinity improved fruit quality and nutritional composition in the first sampling, while no significant improvement was recorded in the second and third sampling. The lack of differences between treatments could be related to the fact that salt stress tolerance increased as a result of exposure to prior stress in the first sampling, after which the plant had adapted. In line with the previous experiment, Petropoulos et al. (2017) showed that increasing salinity from 1.8 to 6.0 dS m⁻¹ had a beneficial effect on sugars, ascorbic acid as well as on α -tocopherol contents in *Cichorium spinosum*, whereas a further increase of nutrient solution salinity (8.0 dS m⁻¹) had a negative effect on specific quality parameters tested. The sugar content of red pigmented lettuce leaves grown in media containing NaCl (EC = 12.6 dS m⁻¹) or seawater (EC = 10.6 dS m⁻¹) was two-fold higher than the control treatment (EC = 1.3 dS m⁻¹) (Sakamoto et al., 2014). In the same study, red leaf lettuce grown under NaCl or seawater contained higher amount of anthocyanins, whereas only lettuce plants irrigated with seawater incurred a significant increase in photosynthetic pigments (i.e., chlorophylls and carotenoids). Additionally, Neocleous et al. (2014) reported that reduced yield of baby lettuce grown in a floating system with gradient NaCl concentrations (5, 10, and 20 mM NaCl) could be at least partly compensated by an increase in anthocyanin concentration in red pigmented lettuce as well as an enhancement in freshness in green lettuce leaves. Preharvest nutrient solution salinity (3.8 and 4.8 dS m⁻¹) applied to a floating system improved the properties of fresh-cut lettuce by extending the shelf life of the final product (Scuderi et al., 2011).

It has been also shown that, by increasing salinity (e.g., 30 mM NaCl) in a floating system, it is possible to improve antioxidant activity, total polyphenols, chlorogenic acid, cynarin and luteolin contents in leaves of both artichoke and cardoon (Colla et al., 2013a). Increasing the secondary metabolites in leaf extracts is considered of high pharmaceutical and nutraceutical importance since several industries are progressively oriented towards the use of natural compounds rather than conventional synthetic chemicals (Lucini et al., 2016; Rouphael et al., 2016).

Most studies concerning the beneficial effect of nutrient solution EC on vegetable quality were based on experiments in which NaCl was the predominant salt. However, few studies focus on the effects of salinity mediated by major nutrients. For instance, Rouphael et al. (2012c) found that increasing nutrient solution concentration from 4 to 68 mequiv L⁻¹ negatively affected the total polyphenols, chlorogenic acid, cynarin as well as luteolin content in leaves of both cardoon and artichoke. An improvement of leaf quality was obtained at the expense of yield when nutrient solution concentration increased from 4 to 20 mequiv L⁻¹, suggesting that the secondary metabolism of cardoon and artichoke plants was stimulated by low nutrient availability as similarly observed by Krauss et al. (2004). In a similar experiment, increasing the concentration of nutrient solution from 2 to 66 mequiv L⁻¹ (i.e. increasing the EC from 0.3 to 3.6 dS m⁻¹) decreased the content of glucose, fructose, starch and total carbohydrates of *Lactuca sativa* L. var. *acephala* grown in floating system (Fallico et al., 2009a). The authors suggested that the reduction in sugar content under high nutrient concentration could be associated to an increase in tissue respiration. Moreover, the reduced sugar content under high nutrient concentration was accompanied with a high nitrate accumulation in leaf tissues, probably for osmoregulatory purposes (Petropoulos et al., 2016). Fallico and co-workers concluded that the use of 37 and 44 mequiv L⁻¹ as nutrient concentration for the spring and summer seasons, respectively, should be adopted among leafy vegetable growers to improve productivity, but with slight reduction in target nutritional traits.

Taking this background into consideration, the proper management of salt and nutrient concentration could effectively improve vegetable

quality, particularly in hydroponic systems. Since quality improvement is sometimes associated with yield reduction, a compromise is needed to find the *section divina*. However, the qualitative response to salt stress of greenhouse vegetables may depend on several interactive variables, including genetic material, climatic conditions, the phenological stage and duration of the exposure as well as the type of salt source and concentration.

4.2. Management of nutrient solution composition

Management of nutrient solution composition, particularly the effects of primary (i.e., N, P, K), secondary macronutrients (Ca, Mg, S) as well as plant micronutrients (i.e., Fe, Si) is also considered an important crop management practice in both soil and soilless culture for improving product quality (Rouphael et al., 2012a). Flores et al. (2004), revealed significantly increased concentrations of β -carotene, lycopene and lipophilic antioxidant compounds content in pepper with an increase of N up to a certain level, whereas Yasur et al. (2013) did not find any significant effect of N concentration (9.2, 56.2, 102.3 and 158.5 mg L⁻¹) on pepper fruit quality (β -carotene and lycopene content and antioxidant activity). On the other hand, the excessive N fertilizer application can result in undesirable changes of quality characteristics such as decrease in the concentration of soluble sugars, carotenoids and vitamin C, while increasing the nitrates, TA, and acid:sugar ratio, leading to a downgrading of commercial and nutritional quality (Dorais et al., 2008; Parisi et al., 2006; Stefanelli et al., 2010; Wang et al., 2008). The low phytochemicals content of vegetables grown under excessive N application (i.e., over fertilization) could be expected since plant secondary metabolites (e.g. β -carotene, flavonols, lycopene and phenolics) are stimulated under N starvation conditions although the net photosynthesis is not simultaneously reduced (Dorais et al., 2008). It is also interesting to note, that a proper N management under soilless culture can lead to an efficient reduction and accumulation of nitrates most notably present in leafy vegetables (Tomasi et al., 2015). Three strategies have been proposed in the scientific literature to cope with the high nitrate accumulation in leafy vegetables: i) replacing nitrate (e.g., calcium nitrate) with chloride (e.g., calcium chloride), ii) nitrate deprivation several days before harvest (DBH, 2–15 days depending on the species), or iii) partial substitution of nitrate with ammonium nitrogen (Borgognone et al., 2016; Kyriacou and Rouphael, 2018; Santamaria et al., 1998; Tomasi et al., 2015). For instance, Borgognone et al. (2016) found that antioxidant activity, flavonoids and total phenols in cardoon leaf extract increased when nitrate was replaced by 80% chloride (20:80 NO₃⁻ ratio), without having detrimental effect of productivity. In fact, in the presence of high chloride levels root-to-shoot translocation of nitrate could be reduced at the site of entrance into xylem parenchyma cells through competition for the same channel (Rubinigg et al., 2003). Nitrate withdrawal in the solution a few DBH has been successfully used for lowering nitrate content in several leafy vegetables such as cardoon (5–15 DBH; Borgognone et al., 2016) chicory, lamb's lettuce and rocket (2–5 DBH; Gonnella et al., 2004; Santamaria et al., 1998). In addition to low nitrate accumulation, the total phenols and flavonoids contents in cardoon leaf tissue increased linearly after 5, 10 or 15 days of nitrate withdrawal in the nutrient solution (Borgognone et al., 2016). A possible explanation of flavonoids synthesis and accumulation under N deficiency could be the activation of the flavonoids pathway through a number of key enzymes and also because flavonoids are actively involved in the ROS scavenging cascade (Bongue-Bartelsman and Phillips, 1995; Takahama and Oniki, 1997). Concerning the effect of different N sources on the quality of vegetables, Zhang et al. (1990) found that nitrate concentration in spinach was decreased by 79–89%, when fertilized with ammonium compared to treatments fertilized with nitrate nitrogen. Furthermore, Heeb et al. (2005) and Siddiqi et al. (2002) indicated that tomato plants receiving 10% of total N in the form of ammonium were characterized by better flavor, presumably through elevated glutamine and glutamate levels.

Potassium has many roles in plant cell, as is considered to be involved in the process of carotenoid biosynthesis by its action on the activity of key enzymes such as phosphofructokinase, pyruvate kinase as well as on precursors of pyruvate and glyceraldehydes 3-phosphate (Bramley, 2002). Increasing K up to 8 mM in nutrient solution increased carotenoids and lycopene content by 40% in comparison to the 0 mM K treatment (Trudel and Ozbun, 1971). Taber et al. (2008) studied the influence of four K fertigation levels (0, 2.5, 5.0 and 10 mM L⁻¹) on lycopene of three commercial determinate tomato cultivars grown under greenhouse conditions. The authors reported that increasing the fertigation level from 0 to 10 mM L⁻¹ increased fruit K concentration by a two-fold and induced a significant increase in fruit lycopene as well as its colorless precursors phytoene and phytofluene in a genotype-dependent manner. Similarly, Almeselmani et al. (2010) confirmed that a significant improvement in greenhouse tomato quality (SSC, ascorbic acid and lycopene content) was observed as K concentration in nutrient solution increased up to 300 mg L⁻¹ (7.7 mM L⁻¹). Finally, Fanasca et al. (2006b) indicated that the highest lycopene concentration was recorded at the red and intense red stages of tomato fruit in plants grown in nutrient solution with high proportion of K. Nevertheless, excess K should be avoided, since it may increase the incidence of blossom-end rot (BER) and other physiological disorders positively correlated with low Ca translocation to the fruit due to competition effect. In a similar experiment, Fanasca et al. (2006a) found that an increase in Ca concentration of the nutrient solution results in a decrease in lycopene concentration (but improved tomato fruit yield) due to antagonism between K and Ca and/or the possible Ca influence on ethylene biosynthesis. In line with the previous study, Paiva et al. (1998) reported a 29% decrease in lycopene content when Ca concentration was increased from 0.2 to 20 mM, with the lowest values recorded at 13.7 mM. Moreover, Subbiah and Perumal (1990) reported that foliar Ca spray applications at 0.1–0.3% increased vitamin C content in tomato by 49%, confirming the positive relationship between Ca and vitamin C levels in tomato fruit grown under different climatic conditions (Bangerth, 1976; Premuzic et al., 1998).

Concerning the influence of Mg on the biosynthesis of antioxidants in vegetables, Fanasca et al. (2006a) demonstrated the positive effect of high Mg proportion in the nutrient solution on hydrophilic antioxidants such as caffeic acid, as well as on the total antioxidant activity. The former beneficial effect could be attributed to high demands of plants for Mg due to increased activity of glutamine synthetase, which is considered a key enzyme that regulates ammonia assimilation within the chloroplasts (Marschner, 1995).

4.3. Biofortification

Human body deficiencies in micronutrients, also known as *hidden hunger*, have become a serious nutritional issue affecting one-third of human population in developing countries of Africa, Asia and Latin America (White and Broadley, 2005). Biofortification of vegetable crops with these essential and/or beneficial micronutrients may represent a promising approach for providing the human diet with selenium (Se), iodine (I), zinc (Zn), iron (Fe) and silicon (Si) (Carvalho and Vasconcelos, 2013; White and Broadley, 2005). Three methods of biofortification in essential and/or beneficial micronutrients have been used for greenhouse vegetables so far, namely the application of the fore-mentioned nutrients with side dressing near the root, with foliar sprays and more efficiently with application in nutrient solution in hydroponic culture (Puccinelli et al., 2017a; Wiesner-Reinhold et al., 2017).

As Se is lacking in many human diets, consumption of vegetables containing Se has raised a lot of interest among scientists in the last decade. The Food and Nutrition Board of the Institute of Medicine has suggested a Recommended Dietary Allowance (RDA) of 55 µg day⁻¹, a daily toxic threshold of 400 µg and also estimated the average dietary intake at which clinical selenosis appears as 1262 µg day⁻¹ (Krinsky

et al., 2000). The addition of sodium selenate at three increasing concentrations (Na₂SeO₄; 4, 8 and 12 mg L⁻¹) to the nutrient solution incurred a dose-dependent increase in the Se uptake rate of basil grown in a floating system, without any detrimental effect on the biomass production (Puccinelli et al., 2017b). Similarly, foliar application of Se at 25 mg m⁻² or 50 mg L⁻¹ did not affect the marketable yield of sweet basil plants (Hawrylak-Nowak, 2013; Mezeyová et al., 2016). The Se concentration in basil leaves (2.8, 7.9 and 16.9 µg g⁻¹ FW, at 4, 8 and 12 mg L⁻¹, respectively) recorded in the former hydroponic experiment was higher than those of basil plants sprayed foliarly (Mezeyová et al., 2016). Presumably, the constant contact of the basil root system to Se-enriched solution made floating system more efficient. Similarly, the addition of 0.5 and 1.0 mg Se L⁻¹ (as sodium selenate) in the nutrient solution resulted in an increase in Se concentration in the leaves of chicory and lettuce grown in a floating system accompanied with a positive effect on marketable yield (Malorgio et al., 2009). The authors also demonstrated that both leafy vegetables enriched with Se exhibited a longer shelf-life, in association with lower rates of ethylene biosynthesis. Furthermore, in senescing lettuce plants, Se has been found to mitigate oxidative stress by preventing the decrease in tocopherol concentration and by stimulating the activity of superoxide dismutase (Xue et al., 2001). Even in *Brassica* species the highest concentration of Se has been observed under soilless culture (Wiesner-Reinhold et al., 2017). The authors reported Se concentrations of 1,200–1,800 µg g⁻¹ DW in the floret and leaves of broccoli, up to 1900 µg g⁻¹ DW in rapid cycling cabbage leaves and 1,800–2,000 µg g⁻¹ DW in *Brassica juncea* shoots and seedlings, respectively (Bañuelos et al., 1990; Kopsell and Randle, 1999; Lyi et al., 2005; Pilon-Smits et al., 1999; Ramos et al., 2011; Ximenez-Embun et al., 2004). Differences in accumulation capacity for Se have been reported also in lettuce accessions, confirming the importance of the genetic material in biofortification (Ramos et al., 2011). Another important factor that could affect Se concentration in vegetables is the chemical form, with sodium selenate and sodium selenite being the most used Se-sources for biofortification. In general, vegetables are more susceptible to selenite than selenate (Rios et al., 2008). Plants exposed to selenate rather than selenite can accumulate much more Se in plant tissues, since selenate is taken up actively by the sulfate transporters, compared to the less efficient phosphate transporters used in the uptake of selenite (Wiesner-Reinhold et al., 2017). Therefore, when producing vegetables enriched with Se it is crucial to take into consideration several agronomic and environmental factors such as the concentration of Se in the nutrient solution, the exposure time, the genetic material as well as the growing season in order to avoid toxic conditions that might be observed in the diet of some target population groups (vegetarians, infants and elderly).

Iodine (I) belongs to the group of essential micronutrients in human nutrition since it plays an important role in the thyroid function (White and Broadley, 2005). It is naturally present in fish and dairy products and to a lesser degree in fruits and vegetables. The Food and Nutrition Board of the Institute of Medicine has suggested a Recommended Dietary Allowance (RDA) of 155 µg day⁻¹ for adults. The biofortification of I could be applied in two forms: potassium iodate (KIO₃) and potassium iodide (KI), with the latter being more bioavailable for vegetable crops. Voogt et al. (2010) reported that in both winter and summer growing seasons the application of 0, 13, 39, 65 and 90 or 129 µg iodine L⁻¹, applied as iodide or iodate in the nutrient solution did not affect yield and quality of lettuce. The authors reported that I content in leaf tissue was five-fold higher with iodide than with iodate application and the highest iodide doses in both growing seasons resulted in 653 and 764 µg kg⁻¹ FW. Blasco et al. (2008) also studied the I uptake by lettuce plants grown in solution culture at seven iodide and iodate concentrations (10, 20, 40, 80, 120, 160, and 240 µmol L⁻¹). A significant reduction of biomass was observed in lettuce at iodine doses higher than 40 µmol L⁻¹ when applied as iodide, whereas the iodate concentration had no detrimental effect on biomass, which is similar to the findings of Zhu et al. (2003) on spinach. Simultaneous application

of I and Se has been also suggested as a safe and efficient tool to increase nutritional content of lettuce and spinach in hydroponic systems (Smolen et al., 2014; Zhu et al., 2004). The iodine content in pepper fruits increased with increasing iodide application (0.5, 1.0, 2.5 and 5.0 mg L⁻¹), amounting to 5–19 mg kg⁻¹ DW, equivalent to 350–1330 µg kg⁻¹ FW (Li et al., 2017), in line with the biofortification trials on tomato (Kiferle et al., 2013), indicating that also fruit vegetables can be targeted for iodine biofortification in respect to dietary iodine allowance (i.e. 150 µg day⁻¹). Li et al. (2017) also showed that low-moderate doses of I increased fruit quality parameters in pepper such as soluble sugars and ascorbic acid content.

Barrameda-Medina et al. (2017) indicated that supplementation of 80–100 µM Zn in the nutrient solution can promote a significant increase in Zn concentration in the edible part of *B. oleracea* as well as an important accumulation of total amino acids (Phe, Trp, Leu, Hys, Lys, Arg, Asp, Glu and Gln). Concerning Fe biofortification, Inoue et al. (2000) showed that increasing Fe concentration in the nutrient solution 6 h before harvest induced an increase in foliar Fe content in lettuce. Montesano et al. (2016) demonstrated that soilless cultivation can be successfully adopted for green bean Si biofortification, where 10–25 mg day⁻¹ is recommended. In the fore-mentioned work, the authors indicated that Si concentration in biofortified pods was three times higher than non-biofortified ones with no negative effect on crop performance. Besides the Si concentration of biofortified pods was higher than non-biofortified irrespective of the cooking methods (boiling or steaming). The Si biofortification of six leafy vegetables (basil, chicory, mizuna, purslane, Swiss chard and tatsoi) and their bioaccessibility were also investigated by the same research team (D'Imperio et al., 2016). The addition of Si as potassium metasilicate in the nutrient solution at concentrations of 50 or 100 mg L⁻¹ induced a species-related accumulation of Si (expressed as SiO₂) as follows: 41–294, 23–76, 19–106, 15–93, 17–76 and 18–69 mg kg⁻¹ FW for basil, chicory, mizuna, purslane, Swiss chard and tatsoi, respectively. The results confirm that species selection is important to obtain potential Si biofortified vegetables. Taken all together concerning vegetable biofortification programs, benefits and risks should be accurately evaluated, because the thresholds between deficiency and toxicity of these essential and/or beneficial micronutrients is often very narrow for humans.

4.4. Plant biostimulants

Nowadays diverse formulations of natural substances or compounds and also microorganisms are applied to plants aiming to improve nutrition efficiency, abiotic stress tolerance and crop quality attributes. These substances and microorganisms are generally referred to as plant biostimulants (PBs; Colla and Rouphael, 2015; du Jardin, 2015). PBs include: humic acids, seaweed extracts, protein hydrolysates, mycorrhizal fungi and plant growth promoting rhizobacteria with strains belonging to genera *Azospirillum*, *Azotobacter* and *Rhizobium* spp. (Colla et al., 2014, 2015; Rouphael et al., 2015).

PBs have been claimed to activate under optimal and sub-optimal conditions a series of physiological and molecular mechanisms such as enhancement of photosynthesis, increase of nutrient uptake and translocation and also activation of secondary metabolism, thus stimulating the production of phytochemicals (Colla et al., 2015; Rouphael et al., 2015).

In a recent study, Colla et al. (2017) demonstrated that foliar application of plant-derived protein hydrolysate (PH), plant and seaweed extracts improve marketable yield but differentially modulate fruit quality of greenhouse tomato. The lack of changes between biostimulant-treated and untreated plants on tomato shape index could be expected since it constitutes a morphometric characteristic governed usually by genetic material and little affected by climatic factors and cultural practices (i.e. biostimulant applications), in line with the findings of Rouphael et al. (2017a). Concerning the SSC, Colla et al. (2017) reported that the highest value of SSC were observed when

tomato plants were treated with plant-derived PH. These data were in line with a previous research on pH application, in which foliar application with two biostimulants (alfalfa derived and red grape products), resulted in higher concentration of both glucose and fructose in greenhouse chili pepper (Ertani et al., 2014). Increases in SSC in response to foliar applications of *Aschophyllum nodosum* extract (0.2 and 0.5%; Zheng et al., 2016), humic acid (25, 50 and 100 mg L⁻¹; Aghaeifard et al., 2016; 10 and 20 mL L⁻¹; Yildirim, 2007) and kelp waste extracts (2, 5, 10, 20 and 100%), have been observed in several vegetable crops such as pakchoi, strawberry and tomato. In addition, inoculation with arbuscular mycorrhizal fungi (AMF- mixture of *Rhizophagus intraradices* and *Funneliformis mosseae*) induced accumulation of SSC in red pigmented lettuce cultivar (Baslam et al., 2013a) and zucchini squash (Cardarelli et al., 2010), as well as higher concentrations of glucose and fructose in tomato fruit (Copetta et al., 2011). The authors associated the increased concentrations of SSC along with slightly higher quantities as a consequence of enhanced photosynthetic performance of mycorrhizal plants, irrespective of the growing seasons. Lycopene content was the highest (increased by 125%) when a foliar application of legume-derived pH was delivered, compared to the applications of plant extract, seaweed extracts and non-treated plants (Colla et al., 2017). Similarly, foliar application of a legume-derived pH elicit dose-dependent increases in the synthesis and accumulation of antioxidant compounds (Rouphael et al., 2017a). Compared to the tomato fruit of untreated plants, lycopene content was increased by 35% and 18% in response to foliar application of commercial legume-derived pH delivered at 5.0 and 2.5 mL L⁻¹, respectively. Similarly, the total ascorbic acid in PH-treated plants at 5 mL L⁻¹ was higher by 27% than that recorded in 2.5 mL L⁻¹ treated and untreated tomato plants (Rouphael et al., 2017a). Foliar application of pH may have stimulated the activity of specific enzymes (direct effect) involved in antioxidant homeostasis in cells (Ertani et al., 2014), while it may have also induced changes of K uptake/translocation and leaf coverage (indirect effects). In fact, K is essential for the pyruvic kinase and acetic thiokinase enzymes that are directly involved in lycopene synthesis. Results of the study of Ertani et al. (2014) indicated that green pepper fruits of PH-treated plants (one derived from alfalfa plants and another from red grapes) had higher antioxidant activity and chlorogenic acid, capsaicin and p-coumaric acid contents. Moreover, carotenoids, mainly β-carotene, total phenolics and antioxidant activity also demonstrated a significant increase in response to drench and especially to foliar humic acid applications at different doses (10, 20, 30 and 40 mL L⁻¹; Unlu et al., 2010). Pre-harvest root treatment with various *Aschophyllum nodosum* extract (0.1, 1.0 or 5.0 g L⁻¹) have been also reported to stimulate flavonoids synthesis in spinach thus improving its nutritional quality (Fan et al., 2011a). The treatments of 1.0 and 5.0 g L⁻¹ showed 1.5- and 1.2-fold higher concentrations of flavonoids as compared to untreated plants. This beneficial effect was attributed to increases of chalcone isomerase, one of the key enzymes in the biosynthesis of flavanone precursors and phenylpropanoid plant defense compounds (Fan et al., 2013).

Nutritional improvement by microbial biostimulants in particular mycorrhizal symbionts has been reported on several greenhouse vegetable crops. The antioxidant activity, phenolics and anthocyanins were more abundant in inoculated lettuce plants than in non-inoculated plants, with *Rhizoglossus irregulare* showing stronger ability than *Funneliformis mosseae*, indicating the importance of fungal strain effect on the production of phytochemicals (Avio et al., 2017). Previous studies also showed that mycorrhizal inoculation (*R. intraradices* and *F. mosseae*) could be adopted to obtain lettuce plants enriched with carotenoids, chlorophylls and vitamins (Baslam et al., 2013a), although total phenolics were usually unchanged (Baslam et al., 2013b) except under water stress regime (Baslam and Goicoechea, 2012), or in external leaves of Cos type lettuce (Baslam et al., 2011). Greenhouse strawberry incurred an increase in target phenolic acids, anthocyanins and flavonols such as p-coumaric, cyanidin-3-glucoside, pelargonidin-3-

glucoside, quercetin and kaempferol in response to AMF *Glomus intraradices* inoculation (Castellanos-Morales et al., 2010). Mollavali et al. (2016) investigated the effect of mycorrhizal inoculation (*Diversispora versiformis*, *R. intraradices*, *F. mosseae*) on the qualitative traits of five onion cultivars. The authors showed that mycorrhizal inoculation influenced the activities of catalase (CAT) and peroxidase (POD) as well as flavonol glucosides content by enhancing nutrient uptake and translocation, or by induction of the plant defense system. Among mycorrhizal strains, *D. versiformis* induced an increase in total phenolics and flavonol glucosides contents, as well as in PAL, CAT and POD activities.

Hart et al. (2015) found that inoculation of *R. irregularis* and *F. mosseae* alone or in combination resulted in tomato fruit with more antioxidant capacity, more carotenoids and modulated some volatile compounds (VOC) comparing to untreated plants. The increased carotenoid production in tomato fruits could be attributed to two mechanisms: i) carbohydrate limitation since mycorrhizal fungi could act as carbon drain on the host plant, and ii) hormonal regulation and signaling in plants colonized by AMF (Fiorill et al., 2009; Zhang et al., 2012). AMF inoculation did not affect the flavor compounds analyzed, particularly lipid-derived VOCs, indicating that modification in tomato flavor through alteration of VOCs is likely to be circumstantial and mostly non-significant or minimal in mycorrhizal inoculated tomatoes. Moreover, a significant increase in β -carotene, lycopene and lutein contents were reported in greenhouse tomato when the substrate was amended with a microbial mix containing AMF, different bacteria and green compost (Copetta et al., 2011). In addition to the important role of AMF to enhance plant biosynthesis of secondary metabolites, Battini et al. (2016) demonstrated that plant growth promoting bacteria (PGPB) were also able to modulate the concentration of nutraceutical compounds. In their study, basil plants were inoculated with *R. intraradices* or by a combination of two PGPB isolated from its sporosphere (*Sinorhizobium meliloti* and *Streptomyces* sp.). The PGPB were able to trigger the overexpression of tyrosine-transferase (TAT), hydroxyphenylpyruvate reductase (HPPR) and *p-coumaroyl shikimate 3'-hydroxylase isoform* (CS3' *isol*) genes, 5.7-, 2- and 1.4 fold, respectively. Battini and co-workers concluded that the selected strains of PGPB were able to improve levels of key enzymes for the biosynthesis of rosmarinic acid, an essential functional compound in human diet.

Concerning the antinutrient compounds such as nitrates (Colla et al., 2018), several reports showed that the application of mixed or single amino acids, PH and seaweed extract can reduce the nitrate accumulation of leafy vegetables including lettuce, rocket, Swiss card, spinach and pakchoi, depending on the species, growing conditions and biostimulant applications (Liu and Lee, 2012; Tsouvaltzis et al., 2014; Wang et al., 2007; Zheng et al., 2016). This might be elicited by pH and seaweed extracts through changes in the expression of nitrate transporter gene, as well as through several metabolic pathways involved in N metabolism (nitrate and nitrite reductase, glutamate synthase and glutamine synthetase activities; Colla et al., 2015).

5. Conclusions

The constant pressure on growers and the agro-food industry to produce premium quality greenhouse vegetables with functional properties represent a great challenge for extension specialists and scientists to propose sustainable and effective preharvest methods for the improvement of product quality without compromising yield. These targets can be met through appropriate selection of genotype, grafting combination and management of environmental conditions during plant growth. Finding optimal combinations of these factors to maximize product quality will be a challenge. As documented in this review, many environmental factors and innovative cultural practices such as grafting and plant biostimulants application can greatly impact the nutritional quality of greenhouse vegetables. Vegetable production under hydroponic cultivation seems to be an effective tool for

increasing phytochemicals and essential and/or beneficial micro-nutrients in vegetables (e.g., biofortification) as well as for controlling anti-nutrient accumulation such as nitrates. Several protocols of nutrient solution management are currently available in this respect. Future researchers should focus on: 1) elucidating the Genotype $\times$ Environment $\times$ Management practice interaction in order to select the best combinations, and 2) unravelling the physiological and molecular mechanisms responsible for the enhancement of phytochemicals in vegetable crops under controlled environment systems.

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